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Octopodid Paralarvae from Hawaiian Waters

by

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Abstract. Thirteen types of octopodid paralarvae are recognized from Hawaiian waters, although the adults of only seven species (three are undescribed) are currently known from this area. The most common 11 paralarval types are described; five types can be identified with known adults. Stage II paralarvae differ from Stage I paralarvae by the presence of sucker buds on their arms. The number of suckers in Stage I paralarvae is characteristic for a species, as are their chromatophore patterns. Hatchlings have a high density of integumental pores containing secretory granules that may produce a mucous "drogue" to assist in offshore transport.

INTRODUCTION

The octopodid fauna of Hawaii is poorly known although several species are of economic importance. There has not been a recent review or modern systematic treatment of the group as a whole, and references are few and widely scattered in the literature. SOULEYET (1852) briefly described *Octopus hawaiiensis* in a report of the French *Bonite* expedition. In the same year, GOULD (1852) described and figured *O. ornatus* which had been collected by the U.S. Exploring Expedition. In 1885, HOYLE (see also 1886) described *O. marmoratus* (subsequently synonymized with *O. cyanea* by ROBSON [1929]) from material obtained by the *H.M.S. Challenger* expedition. BERRY (1909) briefly diagnosed *Polypus hoylei* (subsequently placed in the genus *Berrya* by ADAM [1939]) and in 1913, BERRY described *Scaeurgus patagiatus* (subsequently placed in the synonymy of *S. unicirrus* by ROBSON [1929] and by VOSS [1951] but reinstated by TOLL [1988]). In his monograph, BERRY (1914) expanded the documentation of Hawaiian cephalopods, treating all the species recognized at that time. With the exception of a few records listed by BOONE (1938) and VOSS' (1981) review of *O. ornatus,* no other systematic work has been done on Hawaiian octopodids. Several species of *Octopus* not included in the above works, however, are in our collections from Hawaii.

At present the adults of seven species of octopodids are recognized from Hawaii. Four are named, *Octopus cyanea, O. ornatus, Berrya hoylei* and *Scaeurgus patagiatus.* (*Octopus hawaiiensis* has not been reported since its original description and its identity remains uncertain.) Three species are unnamed. One (our Type E) is a shallow-water and intertidal species whose activity pattern was discussed by HOUCK (1977, 1982). Another (our Type I) has permanent flattened tubercles and a low lateral keel on the mantle. This species is commonly captured in trawls by shrimp fishermen (Van Heukelem, University of Maryland, personal communication). A third is a large species, captured on two occasions by fishermen from depths of about 700 m, and is similar in appearance to the giant octopus of the North Pacific, *O. dofleini.* Immature ovarian eggs are 17 mm long indicating the absence of a planktonic stage.

The habits of octopod hatchlings depend greatly on the size of the egg. In most species with small eggs (<4 mm long) the young are planktonic (*i.e.,* they are paralarvae—see YOUNG & HARMAN, 1988) for unknown lengths of time. Five of the seven known Hawaiian octopods lay small eggs. An additional species produces large eggs. The egg size of the one other species is unknown.

The first thorough descriptions of the development of paralarval stages of octopodids were given by NAEF (1923,

1928). At present, only a few species have been studied in detail, even though observations and figures are scattered throughout the literature (see HOCHBERG *et al.*, in press). While no previous studies have examined the paralarvae of Hawaiian octopodids, several figures and photographs of unidentified advanced paralarvae have been published (BERRY, 1914; BOWER, 1981; NEWBERT, 1984).

In this paper, we examine only the Stage I paralarvae. These paralarvae appeared to be sampled quantitatively by our plankton nets while older stages were not. In addition, since the duration of Stage I must be relatively short, we can be assured that all Stage I paralarvae hatched in Hawaiian waters.

MATERIALS AND METHODS

Specimens were obtained from plankton tows taken from both the windward and leeward sides of the island of Oahu and from the windward side of the island of Hawaii. Tows were taken during all seasons and over a period from 1982 to 1987. Nets used were: 1-m ring net, 70-cm Bongo net, 4-m^2 square-frame net, and a 4-m^2 ring net. Net mesh sizes were 333 or 505 μm. The approximately 550 tows filtered more than 2.5×10^6 m^3 of water. Some tows were taken at discrete depths, but most were oblique and fished from 200 or 300 m to the surface. All of the octopodid paralarvae collected were identified. A small proportion of these were used to provide the following descriptions and measurements.

Net-captured material was fixed in 4–5% seawater formalin and subsequently transferred to 40% isopropyl alcohol. Fading of chromatophores occurred in some cases but, in general, fading was not a serious problem. Calcareous sand grains were added to the samples to buffer the alcohol solution. Live eggs of *Octopus cyanea* were obtained from an octopus that had spawned in the Waikiki Aquarium. These were raised through hatching. Preserved eggs and hatchlings of a few other species were obtained from other workers. In a few cases we attempted to rear paralarvae taken from the plankton.

Voucher specimens of all figured species are deposited at the Santa Barbara Museum of Natural History (SBMNH). The remaining material is deposited at the University of Hawaii.

TERMINOLOGY

Where possible we have used the terminology recommended by the Cephalopod International Advisory Council handbook on the identification of young cephalopods (see HOCHBERG *et al.*, in press).

Stage I Paralarva—The stage between hatching and the development of sucker buds on the arms. Hatchlings have a fixed number of fully formed arm suckers but no sucker buds. Considerable growth occurs before sucker buds begin to appear on the arms. The presence of clearly defined sucker buds (Figure 1B) marks the end of this stage and the beginning of Stage II. In lieu of data on the complexities of later development, we consider Stage II to extend through settling and metamorphosis.

Measurements:

Mantle Length (ML)—Length from the most posterior point of the mantle to the most anterior point of the mantle margin measured along the dorsal midline. This definition differs from the standard definition. In paralarvae, unlike adult octopodids, the mantle muscle at the head-mantle fusion is easily seen and accurate measurements can be made. The modified definition applies to all paralarvae measured.

Head Width—Width measured dorsally across the head at the level of the center of the eyes.

Eye Diameter—Anterior-posterior length of the eyeball measured dorsally.

Arm Length—Length of the arm from the center of the mouth to the distal tip of the arm. Since the arms are usually equal in length the measurement of any arm is satisfactory. Often a specific arm cannot be measured owing to its small size (the arms cannot be straightened).

Arm Length Formula—Relative length of the arms beginning with the longest. For example: 3 > 2 > 1 > 4.

Arm Sucker Formula—Relative diameter of the suckers beginning with the largest. Suckers are numbered beginning nearest the mouth.

Indices—Ratio of a given measurement to the mantle length of the same specimen.

Chromatophores (types):

Tegumental—Chromatophores lying in or near the integument. These can be of two types: *superficial* chromatophores of the integument on the exposed outer surfaces of the octopus or *supravisceral* chromatophores of the integument dorsal to the viscera but within the mantle cavity.

Extrategumental—Chromatophores lying in connective tissue well beneath the outermost integument. In the species discussed, this category includes the following chromatophore fields: Dorsal Head, Dorsal Eye and Ventral Head. The separation of the Extrategumental and Tegumental chromatophores becomes arbitrary near the base of the arms.

Chromatophore fields (Figure 2):

Dorsal Arm; Ventral Arm—Chromatophores on the aboral surfaces of each arm of the dorsal or ventral pair of arms. These are commonly in either one or two series (=rows).

Arm Base—A distinctive enlarged chromatophore lying at the aboral base of the arm. Counts given in the description are the total from all arms.

Ventral Mantle, Anterior Margin—Chromatophores lying along or near the anterior margin of the ventral mantle.

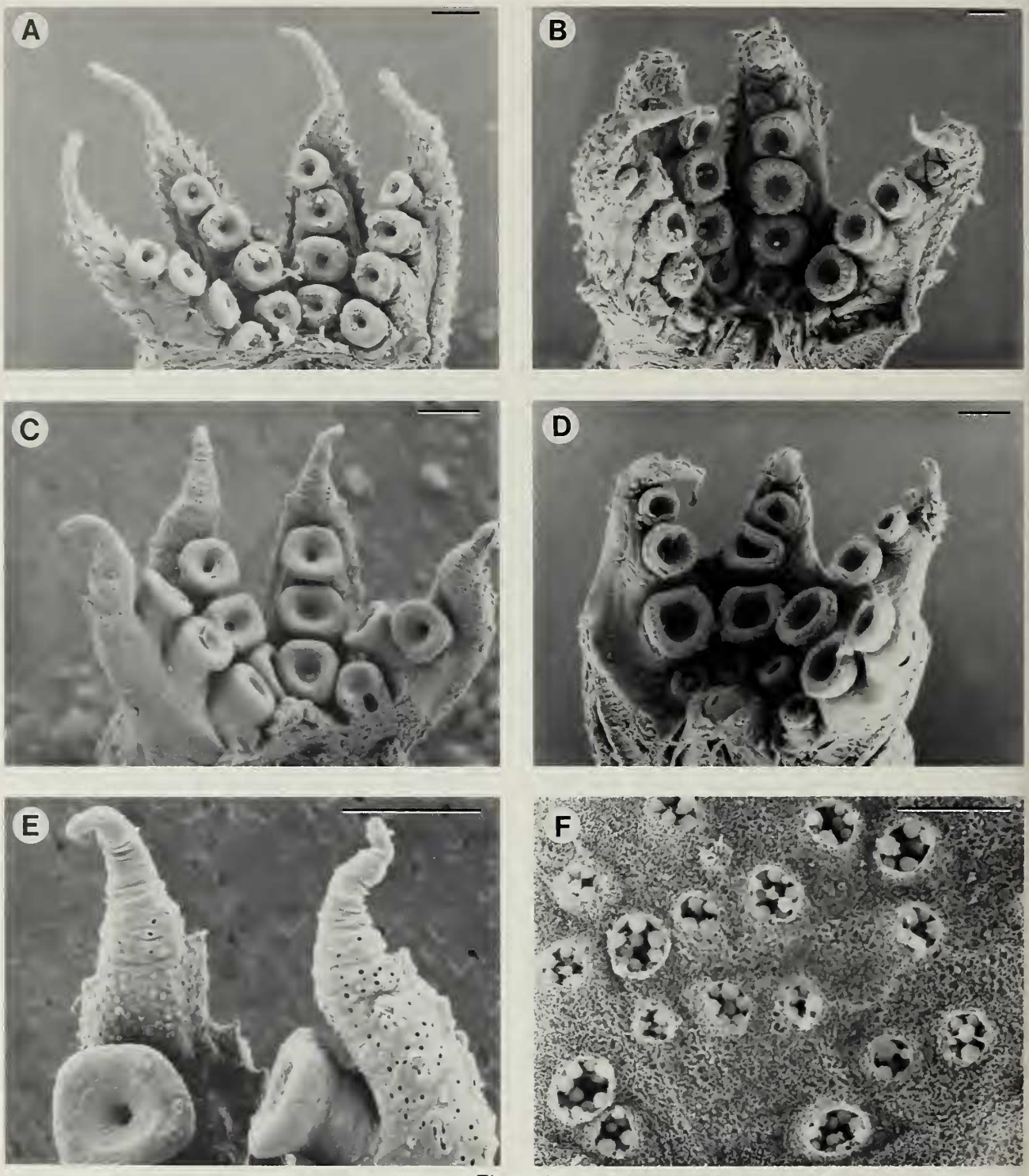


Figure 1

A. Oral view of arms of Type E paralarva (hatchling, 1.6 mm ML) showing four suckers. B. Oral view of arms of early Stage II paralarva of Type E (2.0 mm ML) showing development of sucker buds. C. Oral view of *Octopus cyanea* paralarva (hatchling, 1.2 mm ML) showing three arm suckers. D. Oral view of Type I paralarva (1.2 mm ML) showing relative sucker sizes. E. Arm tips of *O. cyanea* hatchling showing pores on arm surfaces; many of the pores are plugged by secretory products and appear only as rough spots. F. Oral surface of arm of *O. cyanea* hatchling showing high magnification of pores and included secretory spherules. Scale bars: A–E = 0.1 mm, F = 0.01 mm.

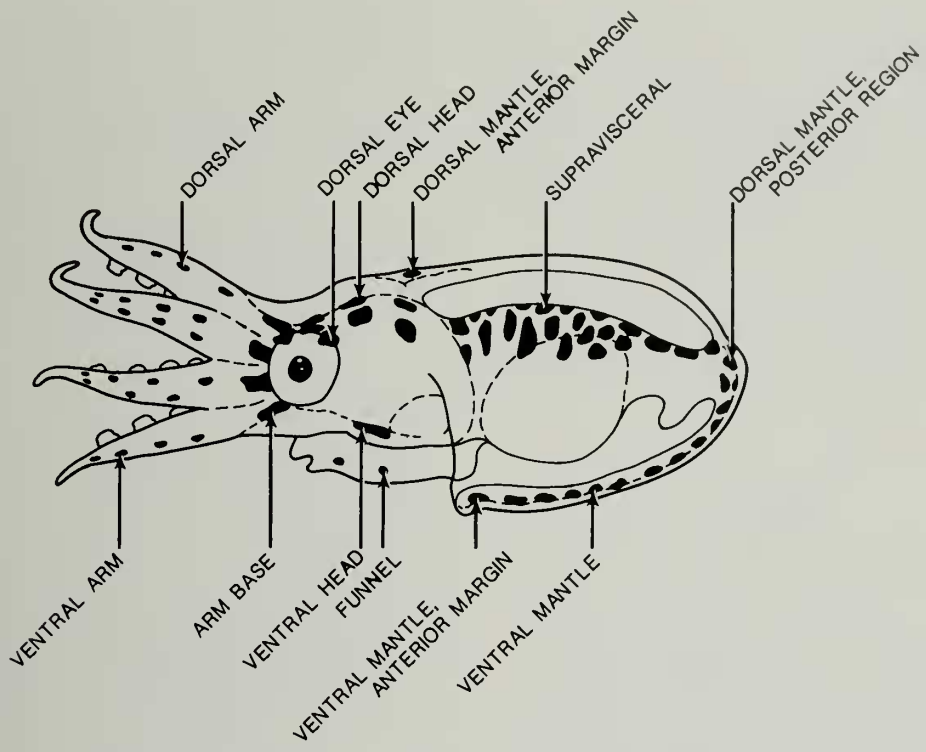


Figure 2

Lateral view of hypothetical Stage I octopodid paralarva illustrating chromatophore fields.

Ventral Mantle, Anterior Region—Chromatophores on the anterior third of the ventral mantle, excluding those of the anterior margin.

Ventral Mantle, Midregion—Chromatophores on the middle third of the mantle measured in the anterior–posterior direction.

Ventral Mantle, Posterior Region—Chromatophores on the posterior third of the ventral mantle.

Posterior Cap—Chromatophores on the posterior dome of the mantle only when they are present in isolation from other mantle regions. In most cases the posterior dome includes chromatophores from the Ventral Mantle, Posterior Region and/or the Dorsal Mantle, Posterior Region.

Dorsal Mantle, Anterior Margin—Discrete band of chromatophores lying along or near the anterior margin of the dorsal mantle muscle.

Dorsal Mantle, Anterior Region—Chromatophores on the anterior third of the dorsal mantle, excluding those of the anterior margin.

Dorsal Mantle, Posterior Region—Chromatophores at the posterior tip of the dorsal mantle. These chromatophores usually are part of a continuous patch that includes chromatophores of the Ventral Mantle regions.

Funnel—Chromatophores on the ventral surface of the funnel. These are counted in groups beginning at the anterior end of the funnel. Thus, 3+2 would mean 3 chromatophores in an anterior band on the anterior tip of the funnel and 2 chromatophores in a band more posteriorly.

Dorsal Head—Deep chromatophores in the connective tissue covering the musculature of the head dorsally. Often the more-posterior chromatophores are partially or completely covered by the dorsal mantle muscle. Chromatophores are counted according to their position on the head from anterior to posterior positions. For example, a 2+4+4 count means 2 anterior chromatophores in a transverse series, 4 intermediate chromatophores in a transverse series, and 4 posterior ones in a transverse series.

Dorsal Eye—Chromatophores lying on the dorsal surface of the eye, occasionally extending partially (well less than half the chromatophore) into the region of the Dorsal Head chromatophores. Often difficult to see against the dark pigment of the eye and can be confused with Dorsal Head chromatophores but are separable by the above definition.

Ventral Head—Deep chromatophores lying on the ventral head musculature.

Supravisceral—Chromatophores mostly in the dorsal integument covering the viscera within the mantle cavity.

Chromatophore arrangements:

Simple band—Transverse series of chromatophores in a single line.

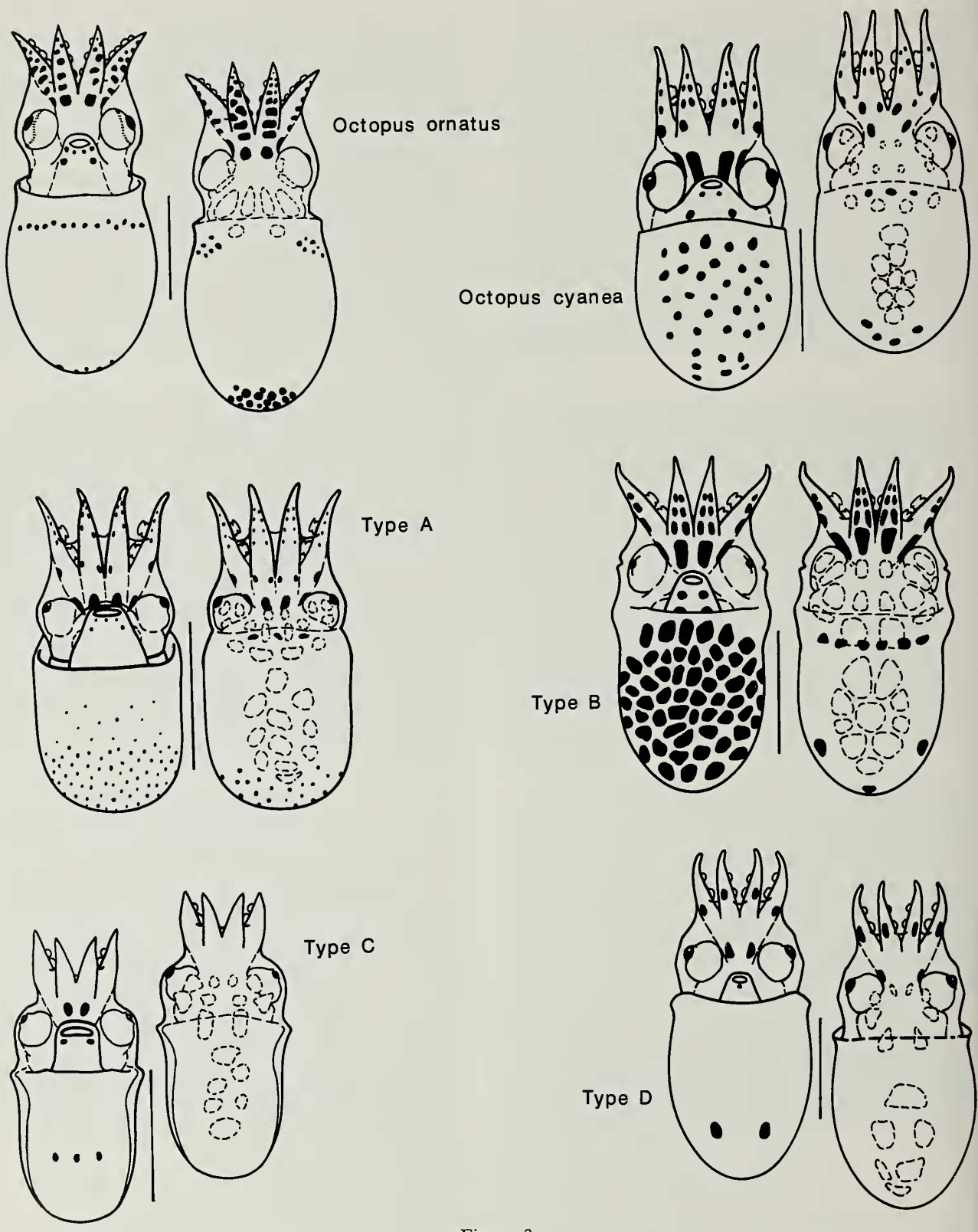


Figure 3

Dorsal and ventral views of Stage I octopodid paralarvae with seven (*Octopus ornatus*) or three (*O. cyanea* and Types A–D) suckers per arm. Scale bar = 1 mm.

Complex band—Transverse series of chromatophores in a single, very irregular line or many (regular or irregular) lines.

Complex stripe—Longitudinal series of chromatophores in a single, very irregular line or many (regular or irregular) lines.

Chromatophore counts:

Mantle, number across—Number of chromatophores across the ventral surface of the mantle. Usually counted in an arbitrary zig-zag line since chromatophores may not be perfectly aligned.

RESULTS

Most measurements of Stage I paralarvae are presented as ranges and indices. Where species change shape considerably over the size range measured, indices (measurement as a fraction of the mantle length) are more useful. Indices are given in parentheses and include the minimum values, the mean (in italics) and the maximum value. Generally, when chromatophores in a particular field are absent, the field is not listed. Occasionally, however, the absence is deemed unusual and the group is listed with a count of zero.

Species Descriptions of Paralarvae

Octopus ornatus

(Figure 3)

Material examined: 23 specimens: 1.9–3.6 mm ML. Voucher SBMNH 35115 (3 specimens).

Body proportions: Mantle Length: 1.85–2.4 mm; Head Width: 1.0–1.6 mm (0.74–*0.82*–0.95); Eye Diameter: 0.3–0.5 mm (0.23–*0.28*–0.33); Arm Length: 0.48–0.80 mm (0.37–*0.42*–0.48); Arm Length Formula: subequal.

Suckers: Number per arm: 7; Largest diameter: 0.14–0.16 mm (0.06–*0.08*–0.09); Smallest diameter: 0.06–0.08 mm (0.03–*0.03*–0.05); Sucker Diameter Formula: $2 = 3 > 1 = 4 > 5 > 6 > 7$, $1 = 2 = 3 > 4 > 5 > 6 > 7$ or $2 > 1 > 3 \geq 4 > 5 > 6 > 7$.

Tegumental chromatophores: Dorsal Arms: one series proximally becoming two distally; Ventral Arms: irregular series proximally, two series distally; Arm Base: 8; Funnel: 5–9 scattered near orifice; Posterior Cap: 20–26 in smallest specimens; Ventral Mantle, Anterior Region: 10–14 across in simple to complex band. Dorsal Mantle, Anterior Region: See **Remarks**; Supravisceral: 8–13 (not shown in figure).

Extrategumental chromatophores: Dorsal Head: 4+2; Dorsal Eye: 3/eye, occasionally 2 or 4/eye; Ventral Head: 0.

Remarks: This species' chromatophore patterns bear little resemblance to those of other species examined here. Chromatophore numbers in nearly all chromatophore fields increase as size increases. In the smallest specimens there are no Dorsal Mantle, Anterior Margin chromatophores. At larger sizes, the simple band of the Ventral Mantle, Anterior Margin field (see Figure 2) becomes complex, broadens and extends dorsally to eventually encircle the mantle near the end of Stage I. Concurrently, chromatophores appear on the Dorsal Mantle, Anterior Margin and, subsequently, extend over the head as size increases. The supravisceral chromatophores are difficult to detect through the mantle. Stage I terminates between 3.0 and 3.2 mm ML.

We have obtained eggs of *Octopus ornatus* preserved in Bouin's solution from J. Arnold (University of Hawaii). The eggs were in an early stage of development and measured 3.2–3.3 mm in length and about 1.05 mm in width.

Octopus cyanea

(Figures 1C, E, F, 3)

Material examined: 56 specimens: 1.1–2.3 mm ML. Voucher SBMNH 35116 (7 specimens).

Body proportions: Mantle Length: 1.1–2.0 mm; Head Width: 1.0–1.6 mm (0.74–*0.82*–0.95); Eye Diameter: 0.3–0.5 mm (0.23–*0.28*–0.33); Arm Length: 0.48–0.80 mm (0.37–*0.42*–0.48); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.4 mm (0.07–*0.1*–0.12); Smallest diameter: 0.10–0.14 mm (0.07–*0.08*–0.10); Sucker Diameter Formula: $1 = 2 > 3$.

Tegumental chromatophores: Dorsal Arms: two series, 3 or 4 pairs; Ventral Arms: two series, 2–4 pairs; Arm Base: 6; Funnel: 2+2, rarely 3+2; Dorsal Mantle, Anterior Margin: simple band, 2 or 3; Posterior Region: 4–6; Ventral Mantle, Anterior Margin: 5, occasionally 4; Midregion: 6 across, occasionally 4, 5, or 7; Supravisceral: 8–10.

Extrategumental chromatophores: Dorsal Head: 4+4+2; Dorsal Eye: 2/eye; Ventral Head: 2.

Remarks: The unusual number of arm base chromatophores (6), while difficult to count, is an important systematic character. Chromatophores of the ventral arms are more vivid than those of the dorsal arms. Chromatophores of the Dorsal Mantle, Anterior Margin are difficult to see and among the first to fade in preservation. Occasionally a few small tegumental chromatophores are present on the head between the eyelids and arms. Stage I terminates between 1.6 and 1.8 mm ML.

Type A

(Figure 3)

Material examined: 11 specimens: 1.2–2.3 mm ML. Voucher SBMNH 35117 (5 specimens).

Body proportions: Mantle Length: 1.2–1.6 mm; Head Width: 1.05–1.25 mm (0.75–*0.82*–0.92); Eye Diameter: 0.30–0.35 mm (0.21–*0.24*–0.29); Arm Length: 0.50–0.72 mm (0.37–*0.44*–0.51); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.10–0.12 mm (0.07–*0.08*–0.08); Smallest diameter: 0.08–0.09 mm (0.06–*0.06*–0.07); Sucker Diameter Formula: 1 = 2 > 3.

Tegumental chromatophores: Dorsal Arms: two series, 4 or 5 pairs; Ventral Arms: two series, 4 or 5 pairs; Arm Base: 8; Funnel: typically 3+2, other patterns include 3+1, 4+1, 3+2, 4, 2+2; Dorsal Mantle, Anterior Margin: 3 or 4 across in simple band; Dorsal Mantle, Posterior Tip: 20–25; Ventral Mantle, Anterior Margin: 0; Ventral Mantle, Midregion: 12–15 across; Supravisceral: 11–15.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3, occasionally 4; Ventral Head: 2.

Remarks: Dorsal Head chromatophores are especially vivid. Funnel chromatophores are minute and mostly concentrated at the orifice. The anterior region of the ventral mantle is bare or has only a few chromatophores. The mantle chromatophores are very small and extend over the Posterior Region of the mantle. A few small superficial chromatophores are found over the anterior eye region. Stage I terminates between 1.7 and 1.8 mm ML.

Type B

(Figure 3)

Material examined: 18 specimens: 1.1–2.2 mm ML. Voucher SBMNH 35118 (6 specimens).

Body proportions: Mantle Length: 1.25–1.55 mm; Head Width: 1.20–1.45 mm (0.86–*0.93*–0.97); Eye Diameter: 0.35–0.45 mm (0.28–*0.30*–0.31); Arm Length: 0.62–0.92 mm (0.48–*0.56*–0.62); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.14 mm (0.08–*0.09*–0.10); Smallest diameter: 0.10 mm (0.06–*0.07*–0.08); Sucker Diameter Formula: 1 ≥ 2 > 3.

Tegumental chromatophores: Dorsal Arms: two series, 3–5 pairs; Ventral Arms: two series, 3 or 4 pairs; Arm Base: 8; Funnel: 2+2+2, 1+2+2 or 2+1+2, occasionally 2+2 or 2+3; Dorsal Mantle, Anterior Margin: 4–6 across in simple band, occasionally 3; Dorsal Mantle, Posterior Region: few; Ventral Mantle, Anterior Margin: 2–6 across; Ventral Mantle, Midregion: 9–12 across; Supravisceral: 8–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3, occasionally 4; Ventral Head: 2.

Remarks: This species is most easily confused with Type A but can be separated by the arrangement of chromatophores on the Funnel and Ventral Mantle fields and by the larger size of the Ventral Mantle chromatophores. In addition, in this species the Posterior Region of the mantle is generally bare or contains only a few, scattered, large chromatophores. In Type A the Posterior Region is covered with numerous small chromatophores.

Dorsal Head chromatophores are especially large and vivid. Funnel chromatophores are all large and none are on the orifice. A few small superficial chromatophores may be present over the anterior eye region. Stage I terminates at 1.6 mm ML.

Type C

(Figure 3)

Material examined: 40 specimens: 1.0–3.6 mm ML. Voucher SBMNH 35119 (6 specimens).

Body proportions: Mantle Length: 1.3–1.5 mm; Head Width: 0.95–1.3 mm (0.70–*0.82*–0.88); Eye Diameter: 0.35–0.50 mm (0.25–*0.31*–0.38); Arm Length: 0.54–0.70 mm (0.40–*0.45*–0.54); Arm Length Formula: 3 > 2 > 1 > 4.

Suckers: Number per arm: 3; Largest diameter: 0.12–0.14 mm (0.08–*0.10*–0.11); Smallest diameter: 0.08–0.10 mm (0.06–*0.06*–0.08); Sucker Diameter Formula: 1 > 2 > 3.

Tegumental chromatophores: Dorsal Arms: 0 in youngest; Ventral Arms: variable; Arm Base: 4, all ventral; Funnel: 2, occasionally 3; Ventral Mantle, Midregion: 2–4 across in simple band; Supravisceral: 6 or 7.

Extrategumental chromatophores: Dorsal Head: 2+4+2, occasionally 4+2; Dorsal Eye: 1, occasionally 2; Ventral Head: 0, occasionally 2.

Remarks: The few, characteristic Ventral Mantle chromatophores frequently were difficult to detect. The diagnostic larger size of arm III was also difficult to detect in the smallest specimens. This arm becomes progressively longer in larger specimens. Ventral Arm chromatophores are usually difficult to see or are absent in the youngest specimens. Sometimes a small chromatophore can be found on each side of each ventral arm indicating a future double series. This feature may be more easily seen on arm III although this arm often has an additional single proximal chromatophore in the midline. If only the latter is detected one could mistakenly conclude that the arm will develop a single series of chromatophores. The youngest specimens can be confused with Type D when the arm length or ventral chromatophore patterns prove difficult to distinguish. However, in these cases, the patterns of Dorsal Head chromatophores can separate these species. Occasionally in Type C paralarvae the anterior set of Dorsal Head chromatophores is missing. The chromatophore count then becomes 4+2 which can be confused with the 2+2+2 count of Type D. Type D, however, never has the first two series fully aligned into a simple band. Stage I of Type C terminates at 1.4–1.5 mm ML. The large arm III develops buds first. Other arms develop buds between 1.6 and 1.8 mm ML. This type of paralarva is commonly referred to as a "macrotritopus."

Type D

(Figure 3)

Material examined: 57 specimens: 1.0–4.0 mm ML. Voucher SBMNH 35120 (11 specimens).

Body proportions: Mantle Length: 1.0–2.0; Head Width: 0.65–1.40 mm (0.65–*0.81*–1.27); Eye Diameter: 0.22–0.50 mm (0.21–*0.25*–0.29); Arm Length: 0.32–0.68 mm (0.31–*0.34*–0.37); Arm Length Formula: subequal.

Suckers: Number per arm: 3; Largest diameter: 0.08–0.12 mm (0.06–*0.07*–0.07); Smallest diameter: 0.06–0.12 mm (0.05–*0.06*–0.07); Sucker Diameter Formula: 1 = 2 ≥ 3.

Tegumental chromatophores: Dorsal Arms: one series, number increases with size; Ventral Arms: one series, number increases with size; Arm Base: 4; Funnel: 2, occasionally 1; Ventral Mantle, Posterior Region: 2; Supravisceral: 5–9.

Extrategumental chromatophores: Dorsal Head: 2+2+2; Dorsal Eye: 1; Ventral Head: 0.

Remarks: Chromatophores are large but generally faint. The Arm Base chromatophores are located at the juncture of arms I and II and at the juncture of arms III and IV. All arms have a single chromatophore proximally in the aboral midline in the smallest specimens, although these may be difficult to see. This becomes a diagnostic single series on each arm in older paralarvae. The diagnostic pair of Ventral Mantle, Posterior Region chromatophores is often difficult to see, as well. This species is most easily confused with young Type C paralarvae. (See **Remarks** under that species). Stage I terminates at 2.0 mm ML.

Type E

(Figures 1A, B, 4)

Material examined: 17 specimens: 1.4–2.9 mm ML. Voucher SBMNH 35121 (6 specimens).

Body proportions: Mantle Length: 1.4–2.1 mm; Head Width: 1.05–1.25 mm (0.56–*0.71*–1.00); Eye Diameter: 0.35–0.45 mm (0.21–*0.27*–0.33); Arm Length: 0.56–0.92 mm (0.35–*0.46*–0.57); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.14–0.18 mm (0.08–*0.10*–0.12); Smallest diameter: 0.10–0.12 mm (0.06–*0.07*–0.08); Sucker Diameter Formula: 2 > 1 = 3 > 4 or 2 ≥ 3 ≥ 1 ≥ 4.

Tegumental chromatophores: Dorsal Arms: two series, 4 or 5 pairs; Ventral Arms: two series, 3 pairs; Arm Base: 8; Funnel: 2+2+2, occasionally 1+2+2 or 3+2+2; Dorsal Mantle, Anterior Margin: 3 or 4 across in simple band; Dorsal Mantle, Posterior Region: 8–20; Ventral Mantle, Anterior Margin: 4–7; Ventral Mantle, Midregion: 5–7 across; Supravisceral: approximately 20–30.

Extrategumental chromatophores: Dorsal Head: 2+4+4, occasionally 2+3+4 or 3+4+4 or up to 15 arranged irregularly; Dorsal Eye: 3–5; Ventral Head: 2.

Remarks: The mantle is distinctly elongate; this feature combined with the large number of supravisceral chromatophores is diagnostic for Type E species. The chromatophores on the ventral mantle form a broad complex stripe. The basic 2+4+4 Dorsal Head chromatophore pattern is often obscured as size increases by additional Dorsal Head chromatophores. A few small superficial chromatophores may be present over the anterior eye region. Stage I terminates between 2.0 and 2.5 mm ML.

Preserved eggs and hatchlings with color photographs were obtained from B. Houck, presently at the University of Portland, Oregon. These allowed positive identification with adults commonly known as the "crescent octopus." Eggs are about 3 mm in length (Houck, 1977).

Type F

(Figure 4)

Material examined: 6 specimens: 1.1–2.0 mm ML. Voucher SBMNH 35122 (3 specimens).

Body proportions: Mantle Length: 1.1–1.6 mm; Head Width: 0.9–1.2 mm (0.67–*0.72*–0.76); Eye Diameter: 0.34–0.45 mm (0.23–*0.27*–0.32); Arm Length: 0.45–0.85 mm (0.35–*0.41*–0.52); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.10–0.13 mm (0.07–*0.08*–0.09); Sucker Diameter Formula: 1 = 2 = 3 ≥ 4.

Remarks: Generally no chromatophores can be detected. One specimen (1.6 mm ML), however, had some faint chromatophores in the following pattern: one at the base of each arm I, two in one series on each arm III, and three in one series on each arm IV. Dorsal Head chromatophores were 2+2 and one chromatophore lay over each eye. About 8–10 supravisceral chromatophores were present. Köllikers organs are numerous. Stage I terminates between 1.6 and 2.0 mm ML.

Type G

(Figure 4)

Material examined: 3 specimens: 1.3–2.3 mm ML. Voucher SBMNH 35125 (1 specimen).

Body proportions: Mantle Length: 1.3–2.3 mm; Head Width: 1.2–1.6 mm (0.71–*0.81*–0.88); Eye Diameter: 0.35–0.55 mm (0.24–*0.26*–0.27); Arm Length: 0.70–1.10 mm (0.33–*0.46*–0.57); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.19 (2.3 mm ML specimen); Smallest diameter: 0.12 (2.3 mm ML specimen); Sucker Diameter Formula: 1 = 2 = 3 ≥ 4 or 2 = 3 > 1 > 4.

Tegumental chromatophores: Dorsal Arms: irregular between one and two series; Ventral Arms: irregular between one and two series; Arm Base: uncertain; Funnel: 0; Dorsal Mantle, Anterior Margin: 0; Dorsal Mantle, Anterior Region: 7–9 across in a complex band that is continuous with the Ventral Mantle, Anterior Region; Ventral Mantle, Anterior Region: 7–13 across in wide complex band; Supravisceral: 6–8 (not shown in Figure 4).

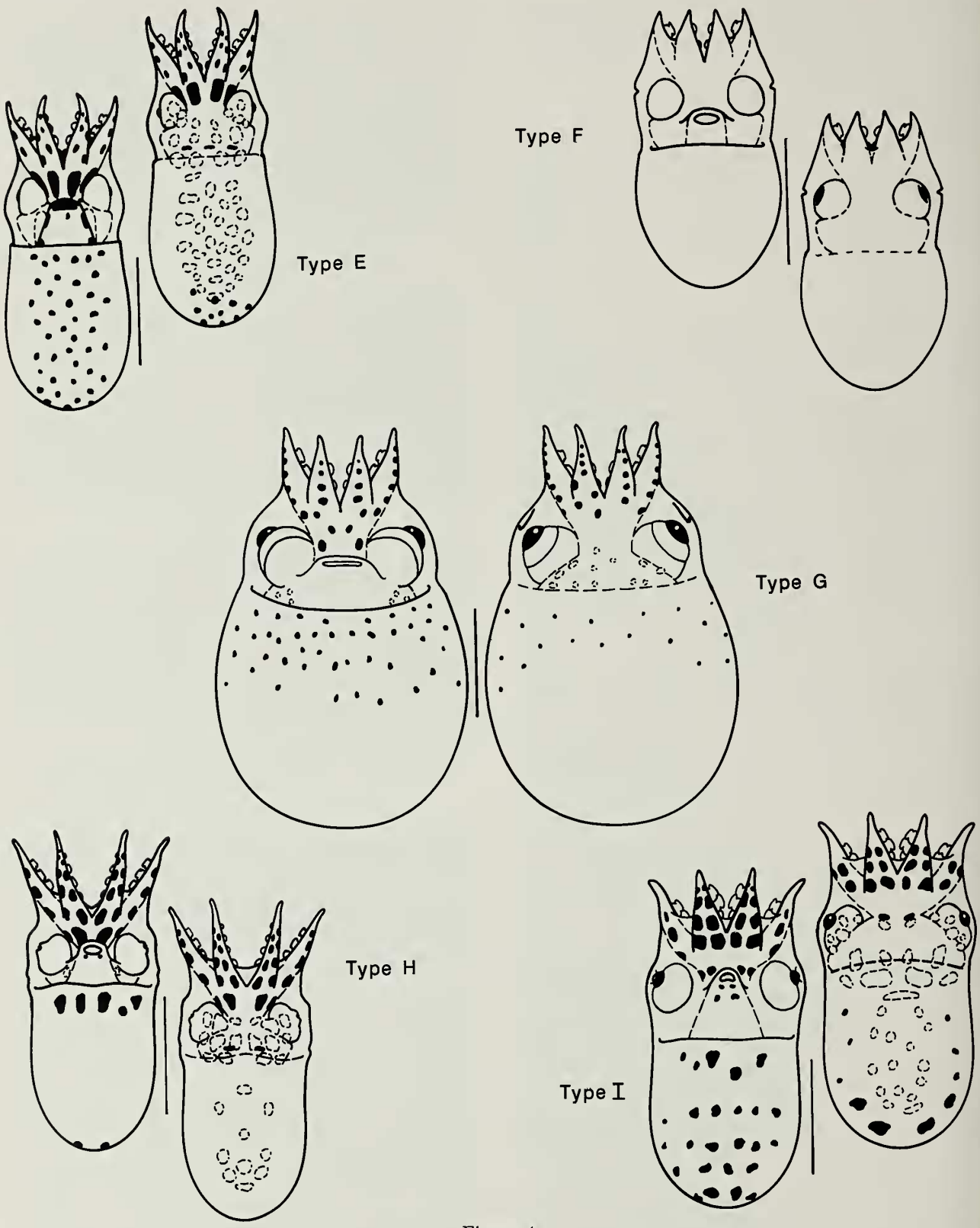


Figure 4

Dorsal and ventral views of Stage I octopodid paralarvae with four suckers per arm. Scale bar = 1 mm.

Extrategumental chromatophores: Dorsal Head: about 12 in irregular arrangement; Dorsal Eye: uncertain; Ventral Head: about 8, scattered.

Remarks: Some chromatophores had faded by the time they were counted, resulting in low or zero counts in some cases. When all chromatophores are faded, this species is virtually inseparable from Type D paralarvae. Both are squat and rather gelatinous. The size at which Stage I terminates is unknown.

Type H

(Figure 4)

Material examined: 43 specimens: 1.0–4.0 mm ML. Voucher SBMNH 35123 (11 specimens).

Body proportions: Mantle Length: 1.0–2.0 mm; Head Width: 1.00–1.50 mm (0.75–*0.85*–1.00); Eye Diameter: 0.25–0.40 mm (0.20–*0.24*–0.29); Arm Length: 0.24–0.36 mm (0.18–*0.20*–0.24); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.08–0.12 mm (0.05–*0.08*–0.09); Smallest diameter: 0.04–0.08 mm (0.03–*0.04*–0.06); Sucker Diameter Formula: 2 > 1 = 3 > 4.

Tegumental chromatophores: Dorsal Arms: two series, 4 pairs; Ventral Arms: two series, 4 pairs; Arm Base: 8; Funnel: 2+2, occasionally 2; Dorsal Mantle, Anterior Margin: 2–4 across in simple band; Ventral Mantle, Anterior Margin: 5 or 6, occasionally 7 across in simple band; Ventral Mantle, Posterior Region: 2 or 3; Supravisceral: 12–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3; Ventral Head: 2.

Remarks: All chromatophores are large and vivid. Eye chromatophores are difficult to see against the dark eyes. Distal Funnel chromatophores are very small and lie near the orifice. Posterior Funnel chromatophores, when present, are only slightly larger and lie near the others. One or two small superficial chromatophores are often present anterior to the eye opening. The Ventral Mantle, Anterior Margin chromatophores are diagnostic. Stage I terminates between 2.0 and 4.0 mm ML.

Type I

(Figure 4)

Material examined: 22 specimens: 1.1–2.2 mm ML. Voucher SBMNH 35124 (6 specimens).

Body proportions: Mantle Length: 1.1–2.0 mm; Head Width: 1.05–1.25 mm (0.55–*0.79*–1.05); Eye Diameter: 0.35–0.45 mm (0.20–*0.27*–0.35); Arm Length: 0.62–0.74 mm (0.39–*0.51*–0.68); Arm Length Formula: subequal.

Suckers: Number per arm: 4; Largest diameter: 0.16–0.23 mm (0.11–*0.14*–0.17); Smallest diameter: 0.10–0.12 mm (0.06–*0.08*–0.10); Sucker Diameter Formula: 2 > 3 > 4 > 1.

Tegumental chromatophores: Dorsal Arms: two series, 2 or 3 pairs; Ventral Arms: two series, 3 or 4 pairs; Arm Base: 8; Funnel: 2+2, occasionally 2; Dorsal Mantle, Anterior Margin: 0; Dorsal Mantle, Posterior Region: 4–6; Ventral Mantle, Anterior Margin: 3–6; Midregion: 4–6 across; Supravisceral: 12–17.

Extrategumental chromatophores: Dorsal Head: 2+4+4; Dorsal Eye: 3–5; Ventral Head: 0.

Remarks: The small size of sucker No. 1 (proximal sucker) and the large size of sucker No. 2 are diagnostic of Type F paralarvae in Hawaiian waters. Chromatophores are large and vivid, especially so in the fields on the dorsal surfaces. Anterior Funnel chromatophores are very small and located on the funnel orifice. Scattered chromatophores may extend from the Dorsal Mantle, Posterior Region along the dorsolateral margins of the mantle. The number of Dorsal Eye chromatophores increases with size. Stage I terminates between 2.0 and 2.3 mm ML.

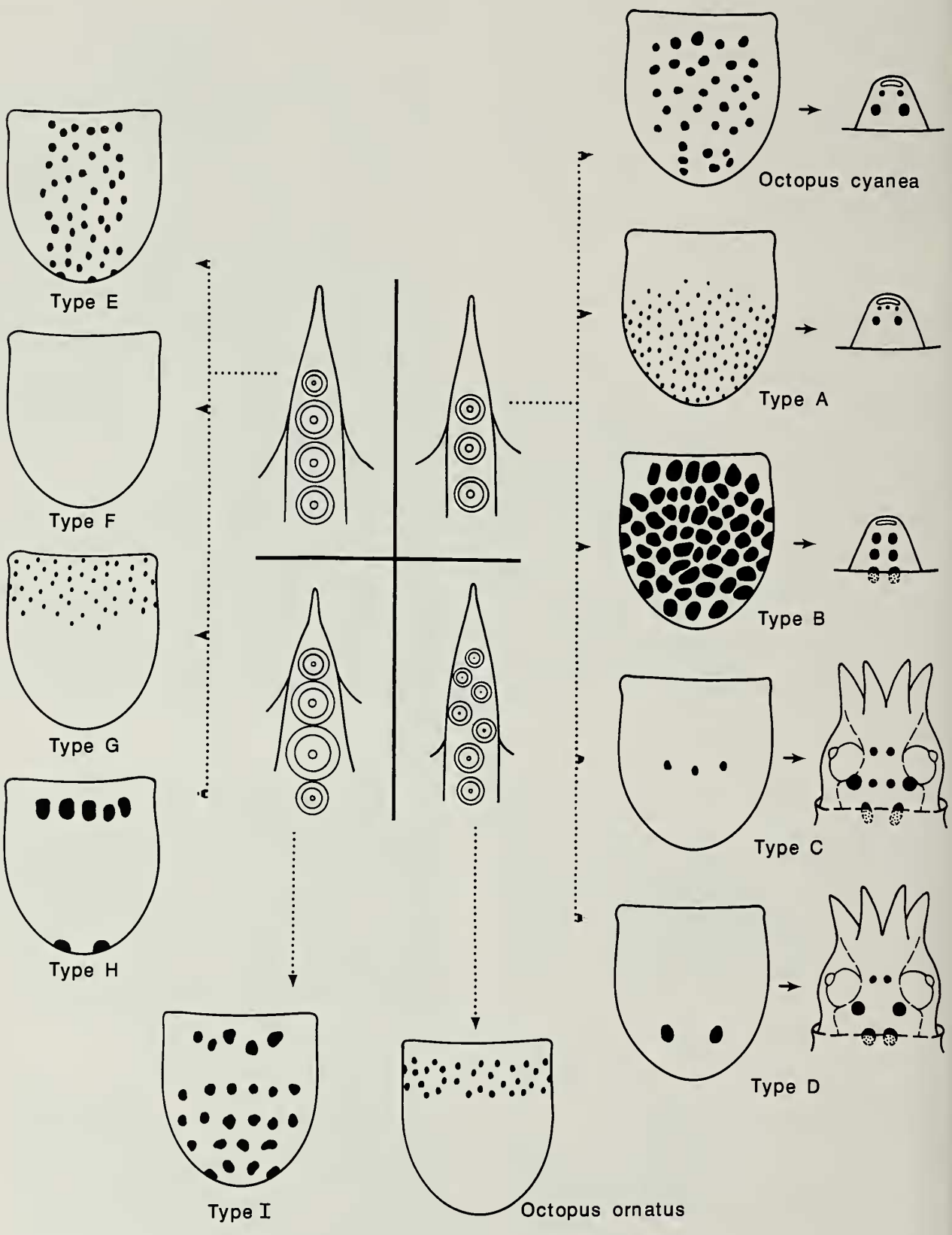
Eggs and their hatchlings were available from J. Arnold who obtained them from W. Van Heukelem. Although labelled as *Scaeurgus*, they probably came from an undescribed species with certain similarities to *Scaeurgus* (Van Heukelem, personal communication). The material, preserved in Bouin's fluid, measured 3.0 mm for eggs near hatching and 1.2–1.3 mm ML for hatchlings. Our smallest specimens taken from the plankton are smaller than this, but this is not surprising considering the variability in size measurements due to state of contraction following fixation.

Older Stages

Our collection of paralarvae between Stage I and settling (metamorphosis) is incomplete. Since little is known for most octopodids regarding the size they can reach while planktonic, the largest identifiable paralarvae that we have in our collections are listed here. These data do not imply size at metamorphosis. *Octopus ornatus*, 7.3 mm ML; *O. cyanea*, 11.0 mm ML; Type A, 6.1 mm ML; Type B, 6.0 mm ML; Type C, 13.5 mm ML; Type D, 6.5 mm ML; Type E, 15.0 mm ML (tentative identification); Type F, 5.5 mm ML; Type G, 5.8 mm ML; Type H, 6.1 mm ML; Type I, 7.7 mm ML.

Other Species

Two additional types of octopodid paralarvae are known to occur in Hawaiian waters but have not been described here. W. Ikehara (Hawaii Division of Aquatic Resources) reported finding a small brooding octopus in intertidal waters on Oahu. He removed the egg string and reared the embryos through hatching. Photographs that he took reveal a paralarva with very different chromatophore patterns from any described here. The arms had chromatophores in 2 rows; the ventral mantle was covered with


Type E
Type F
Type G
Type H
Type I
Octopus ornatus
Octopus cyanea
Type A
Type B
Type C
Type D

numerous small, densely packed chromatophores; the dorsal mantle had many small but more scattered chromatophores; about 50 supravisceral chromatophores appeared to be present. The identity of the adult is unknown, but fishermen report that it is fairly common in the intertidal zone throughout Hawaii.

The other undescribed paralarva was taken in a plankton tow and is very similar to Type F, but was more gelatinous and had a slightly more restricted mantle opening as well as many, very tiny, faint chromatophores on the head, funnel, and mantle. Our single specimen was just beyond Stage I and most chromatophores had faded before we were able to record the patterns.

Integumental Pores

We examined some paralarvae with the scanning electron microscope in order to photograph the sucker arrangement and to demonstrate the distinctive appearance of sucker buds that mark the end of Stage I (Figures 1A–D). This examination enabled us to examine other features as well. (1) We expected to find sensory organs on the peculiar attenuate arm tips, but did not. The function of these elongate, bare arm tips is unknown. (2) We observed large numbers of pores covering the arms, head, and mantle. In many areas the pore apertures constitute over 10% of the body surface (Figure 1E). High magnification of the pores reveals small spheres in the apertures (Figure 1F). We assume that the pores are the openings of mucus-secreting organs and the spheres are the secretory products before expansion in water. The high pore density was apparent only on paralarvae hatched in the laboratory. We searched the surfaces of several types of net-caught paralarvae of various sizes and, while some pores could be found, densities were always low.

DISCUSSION

We believe that all the paralarval types described here represent valid species. All are characterized by a suite of consistent characters. Further, we are confident that they represent Hawaiian species. Although the duration of Stage I is unknown for most species, it is probably very short. For example, sucker buds appear on the arms of three-day-old hatchlings of *Octopus bimaculatus* (AMBROSE, 1981).

Nearly all Stage I paralarvae of the Hawaiian octopodid species can be recognized easily by their chromatophore patterns. Virtually every field of chromatophores exhibited specific characteristics in some species. The Ventral Mantle field, however, showed the greatest range of chromatophore patterns and was the most useful for identification. Both the pattern and the number of chromatophores (within a specific chromatophore field) were usually distinctive. Pattern changes beyond Stage I paralarvae were not presented in this study but did vary between species. For example, in Type D, except for increases in chromatophore numbers on the longer arms, the pattern remained unchanged up to at least 6 mm ML, while in Type B increases in numbers of chromatophores, especially in Dorsal Mantle chromatophores, began by 2–3 mm ML.

The number of suckers per arm in Stage I paralarvae also proved to be a valuable feature for identification. Of the 11 species where Stage I paralarvae were examined, five species had three suckers per arm, five species had four suckers, and one species had seven suckers. This character is unambiguous, easily detected, and because it separates major suites of species, it is extremely useful for identification. Sucker size was diagnostic in one species (Type I). In the younger stages, only one species (Type C: "macrotritopus") had a distinctive arm formula.

These characters are suitable for constructing a key based on icons. Such a key (Figure 5) is far simpler and faster to use than a typical dichotomous key. One simply follows the arrows from the original choice of four drawings. Secondary characters are indicated by non-branching arrows.

The distribution of Kölliker's organs provided another potentially valuable systematic character. The high density of these bristlelike structures, especially on the ventral surfaces of the head, was characteristic of several species (*e.g.*, Types E and F). However, intraspecific variations were considerable and detection of the organs proved to be difficult. Thus, we made no attempt to quantify this character, and we used it only as a guide when chromatophore patterns had faded.

The paralarvae of only three types, *Octopus cyanea* and Types E and I, can be connected to adults with certainty (adults of the latter two species are undescribed). In these cases, hatchlings were obtained and examined from known females that spawned in captivity. The only other method of positive identification requires the rearing of advanced paralarvae taken from plankton. We reared Type H for three months and Type D for about six months. Although growth of Type H was minimal during this period, the octopus metamorphosed into its benthic form and displayed distinctive chromatophore patterns and unusual sculpturing. It clearly does not belong to any known Hawaiian species. Type D grew better than Type H in captivity but remained small and nondistinct. It, also, cannot be related to any known species. In regions like Hawaii where adult octopods of many species are scarce and cryptic, rearing

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Figure 5

Key to Hawaiian octopodid paralarvae. Begin by picking the appropriate drawing from the central four, then follow dotted lines and arrows. On the right, secondary characters are shown for species with three arm suckers. Funnel chromatophore patterns must be used with caution due to intraspecific variability (see text).

paralarvae captured in the plankton may ultimately prove to be the more useful technique for paralarval identification.

Distinctive paralarval features suggest adult affinities for a few additional species:

(1) We are confident of the identification of paralarvae of *Octopus ornatus* owing to their similarity to the paralarva of *O. macropus* illustrated by NAEF (1928). The Hawaiian member of the *O. macropus* species complex is *O. ornatus*. Not only do the Hawaiian paralarvae have similar chromatophore patterns, but they also share the same unusual number (7) of Stage I arm suckers.

(2) In the Atlantic, "macrotritopus" paralarvae have been shown to be young of *Octopus defilippi* (HANLON *et al.*, 1980; NESIS & NIKITINA, 1981; HANLON *et al.*, 1985). Although this species is not known to occur in Hawaiian waters, it or a sibling species must be present since our paralarvae (with the exception of differences in chromatophore patterns) are very similar to the macrotritopus previously described. We, therefore, refer specimens of Type C to the *O. "defilippi"* species complex.

(3) BOLETZKY (1977, 1984) described the paralarvae of *Scaeurgus unicirrus* from the Mediterranean and we have examined some of his specimens. The paralarvae of Type F are very similar to these. Unfortunately, the chromatophores of Type F are usually absent (in contrast to the Mediterranean paralarvae). Nevertheless, in one advanced Stage I paralarva some faint chromatophores were present. This paralarva seemed to have a single row of chromatophores on the arms as is characteristic of Mediterranean paralarvae. This is an unusual feature in Hawaiian paralarvae. In addition, both Hawaiian and Mediterranean paralarvae have four suckers in Stage I and high concentrations of Kölliker's organs. We tentatively assign Type F to *Scaeurgus patagiatus*.

The similarity of the paralarvae of *Octopus ornatus* and Type C to their Atlantic siblings suggests that paralarval morphology and chromatophore patterns are conservative and that these characters may be useful in octopodid systematics above the species level.

Our SEM observations of densely packed secretory pores on hatchlings, but not larger paralarvae, are puzzling. Perhaps the secretion of mucus is important either during the late embryonic stages or for a short period after hatching. We suggest that mucous secretions in the latter case might form a "drogue" that would assist the young octopus in remaining near the surface while currents transport it offshore. Hatchlings observed in the laboratory were strongly negatively buoyant and had to swim vigorously to remain near the surface of their container. Mucous secretions have not been observed in laboratory-reared hatchlings, perhaps because water turbulence or aquarium walls destroy any mucous structures. A mucous drogue would require far less energy expenditure than swimming and the motionless, drifting paralarvae might be less conspicuous to predators.

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